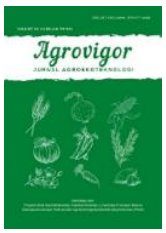
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Article

Boron and Liquid Biofertilizer Modulate Anthocyanin, Flavonoid, and Protein Accumulation in Black Soybean (*Glycine max* (L.) Merr.)

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ABSTRACT

Black soybean (*Glycine max* (L.) Merr.) is an important source of bioactive compounds, particularly anthocyanins and flavonoids, which contribute to seed nutritional quality. This study evaluated the effects of boron (B) and liquid biofertilizer (LBF) application on flavonoid, anthocyanin, and total protein contents in black soybean seeds. The experiment was conducted in Batu, East Java, Indonesia (739 m above sea level) from May to October 2025 using a randomized block design with three replications. Six treatment combinations were applied: B 2.5 kg ha^{-1} + LBF 10 mL L^{-1} (P1), B 2.5 kg ha^{-1} + LBF 15 mL L^{-1} (P2), B 5 kg ha^{-1} + LBF 10 mL L^{-1} (P3), B 5 kg ha^{-1} + LBF 15 mL L^{-1} (P4), B 7.5 kg ha^{-1} + LBF 10 mL L^{-1} (P5), and B 7.5 kg ha^{-1} + LBF 15 mL L^{-1} (P6). The combination treatment significantly affected flavonoid, anthocyanin, and protein contents. The highest flavonoid and anthocyanin contents were obtained under P5, whereas the highest protein content was recorded under P6. These findings indicate that boron and liquid biofertilizer application can influence the biochemical composition of black soybean seeds, with different treatment combinations favoring the accumulation of secondary metabolites and protein.

INTRODUCTION

Black soybean (Glycine max (L.) Merr.) is widely recognized for its high nutritional and functional value, largely attributed to its abundant bioactive compounds. Among these, flavonoids and anthocyanins represent major classes of secondary metabolites that accumulate predominantly in the seed coat, conferring the characteristic dark pigmentation of black soybean seeds (Moon *et al*., 2026). Anthocyanins are responsible for the black–purple coloration and exhibit strong antioxidant activity due to their free-radical scavenging capacity, thereby contributing to protection against oxidative stress and degenerative diseases. Isoflavonoids and other flavonoid derivatives also function as phytoestrogens and demonstrate diverse biological properties, including antioxidant and anticancer activities as well as cardioprotective effects (Patra *et al*., 2023). Beyond their importance in human health, these phenolic compounds play important physiological roles in plant growth, development, and adaptation to environmental conditions.

The biosynthesis of flavonoids and anthocyanins occurs through the phenylpropanoid pathway, a secondary metabolic route closely interconnected with primary metabolism (Rahim *et al*., 2023). This pathway is tightly regulated at both transcriptional and enzymatic levels and is influenced by genetic and environmental factors. The interaction between nutrient availability, carbon–nitrogen metabolism, and secondary metabolite production is fundamental in determining seed quality and phytochemical composition (Larasati *et al*., 2022). Previous studies have extensively investigated flavonoid and anthocyanin accumulation during seed development and maturation; however, the effects of nutrient management strategies on the biosynthesis of these compounds in black soybean remain insufficiently understood (Guo *et al*., 2022).

Environmental conditions and cultivation practices strongly influence the biochemical composition of seeds, including flavonoid and anthocyanin content. Soil fertility, nutrient availability, and agronomic management can modulate metabolic pathways during seed formation, thereby affecting the accumulation of phenolic compounds and the nutritional quality of harvested seeds (Fan *et al*., 2024). Sustainable crop management approaches such as liquid biofertilizers (LBF) have attracted considerable attention because they enhance nutrient uptake efficiency and stimulate plant metabolism through biological nitrogen fixation, phosphate solubilization, and phytohormone production (Allouzi *et al*., 2022). These mechanisms may promote the synthesis of phenylpropanoid-derived metabolites; however, their effects on flavonoid and anthocyanin accumulation in black soybean seeds have not been clearly elucidated.

Micronutrients also play essential roles in regulating enzymatic activities associated with secondary metabolism. Boron (B), for example, contributes to cell wall integrity, membrane stability, carbohydrate transport, and the activation of enzymes involved in phenolic compound biosynthesis, including those within the phenylpropanoid pathway (Dameto *et al*., 2023). Several studies have reported positive effects of boron nutrition on plant growth and reproductive development, yet information regarding its influence on flavonoid and anthocyanin accumulation in black soybean seeds remains limited. Furthermore, little is known about the potential combination between boron application and LBF in regulating secondary metabolite production.

Despite the recognized importance of flavonoids and anthocyanins for the nutritional and functional quality of black soybean, research examining the combined effects of boron and liquid biofertilizer applications on the accumulation of these compounds is still scarce. To date, most studies have focused on either nutrient management or biofertilizer application separately, while the integrated influence of both treatments on phenylpropanoid metabolism has received limited attention. Therefore, this study addresses an important knowledge gap by evaluating the individual and combined effects of boron and liquid biofertilizer on flavonoid and anthocyanin accumulation in black soybean seeds. The findings are expected to provide new insights into nutrient-mediated regulation of secondary metabolism and contribute to the development of sustainable agronomic strategies for enhancing the functional quality of black soybean.

MATERIALS AND METHODS

The research was conducted in Batu Dadaprejo Village, Batu City, East Java, Indonesia, at an altitude of 739 m above sea level, between May and October 2025. The average air temperature during the experimental

period ranged from 22.7°C to 25.1°C. The experimental field is characterized by fertile volcanic soil, which is commonly found in the Batu region and is suitable for soybean cultivation.

Black soybean (*Glycine max* (L.) Merr.) variety Detam 4 Prida was used in this study. The seeds were obtained from the Indonesian Legumes and Tuber Crops Research Institute (Balitkabi), Ministry of Agriculture, Indonesia. The experiment was arranged in a Randomized Block Design (RBD) with three replications.

The treatments consisted of combinations of boron (B) and liquid biofertilizer (LBF): B 2.5 kg ha^{-1} + LBF 10 mL L^{-1} (P1), B 2.5 kg ha^{-1} + LBF 15 mL L^{-1} (P2), B 5.0 kg ha^{-1} + LBF 10 mL L^{-1} (P3), B 5.0 kg ha^{-1} + LBF 15 mL L^{-1} (P4), B 7.5 kg ha^{-1} + LBF 10 mL L^{-1} (P5), and B 7.5 kg ha^{-1} + LBF 15 mL L^{-1} (P6).

Boron was applied using Mahkota Borate fertilizer produced by PT. Wilmar Chemical Indonesia, containing 46% B_2O_3. The liquid biofertilizer used was Explant PHC (Plant Growth Promoter Liquid Biofertilizer), produced by CV Nugraha Makmur Indonesia. According to the product label, the biofertilizer contains beneficial microorganisms including *Pseudomonas* sp. (1 × 10^8 CFU mL^{-1}), *Azotobacter* sp. (9.4 × 10^8 CFU mL^{-1}), *Lactobacillus* sp. (7.9 × 10^8 CFU mL^{-1}), *Azospirillum* sp. (5.5 × 10^8 CFU mL^{-1}), *Rhizobium* sp. (1.3 × 10^8 CFU mL^{-1}), *Nitrobacter* sp. (3.1 × 10^8 CFU mL^{-1}), and *Trichoderma* sp. (2.9 × 10^8 CFU mL^{-1}).

Each experimental plot measured 1.9 m × 1.2 m. Soybean plants were established at a spacing of 50 cm × 25 cm. Each plot consisted of 10 plants, of which four plants were designated as growth samples and six plants were used as harvest samples. Plants were harvested at 76 days after planting (DAP), corresponding to the physiological maturity stage. Seed samples were collected from the designated harvest plants for laboratory analyses. The observed parameters were total flavonoid content, anthocyanin content, and total protein content in the seeds.

Data were analyzed using analysis of variance (ANOVA) for a randomized block design with factorial treatment combinations of boron and liquid biofertilizer (LBF). Prior to ANOVA, the assumptions of normality and homogeneity of variance were evaluated using the Shapiro–Wilk and Levene's tests, respectively. When significant treatment effects were detected ($p < 0.05$), means were separated using Tukey's Honest Significant Difference (HSD) test at the 5% significance level. Statistical analyses were performed using R-Studio.

Total Flavonoid Content Analysis

Total flavonoid content (TFC) was determined using a slightly modified aluminum chloride colorimetric method based on the protocol described by NFRI (1990). Ethanolic extracts (70% ethanol) of black soybean seeds were adjusted to a final concentration of 100,000 μg mL^{-1}. An aliquot of 500 μL of the diluted extract was mixed with 100 μL of 10% aluminum nitrate [$Al(NO_3)_3$] solution and 100 μL of 1 M potassium acetate. The reaction mixture was incubated at room temperature for 40 min to allow the formation of flavonoid–aluminum complexes. Subsequently, the mixture was transferred into a 96-well microplate, and absorbance was measured at 405 nm using a microplate spectrophotometer. Total flavonoid content was quantified using a quercetin standard calibration curve ($y = 0.0066x + 0.0253$, $R^2 = 0.998$). The results were expressed as milligrams of quercetin equivalents per 100 g dry weight (mg QE 100 g^{-1} DW) of seed sample. All analyses were performed in triplicate, and the mean values were used for statistical analysis (Moon *et al.*, 2026).

Total Anthocyanin Content Analysis

Total anthocyanin content (TAC) was determined using the pH differential method following Giusti and Wrolstad (2001). Approximately 0.1 g of sample was extracted with 16 mL of 0.1% HCl in methanol and centrifuged to obtain the supernatant. One milliliter of the supernatant was diluted with 4 mL of 0.1% HCl in methanol. The diluted extract (1 mL) was then divided into two aliquots: the first was mixed with 4 mL of 0.025 M potassium chloride buffer (pH 1.0), and the second with 4 mL of 0.4 M sodium acetate buffer (pH 4.5). Absorbance was measured at 520 and 700 nm using a spectrophotometer, with distilled water as the blank. Total anthocyanin content was calculated according to Giusti and Wrolstad (2001) using the pH differential equation, where MW is the molecular weight of cyanidin-3-glucoside (449.2 g mol^{-1}), DF is the dilution factor, ε is the molar extinction coefficient of cyanidin-3-glucoside (26,900 L mol^{-1} cm^{-1}), and l is the path length (1 cm). Results were expressed as cyanidin-3-glucoside equivalents (C3GE).

Anthocyanin content (mg L^{-1}) = [(A520 − A700)pH1.0 − (A520 − A700)pH4.5] × MW × DF × 1000 / (ε × l).

The calculated values were subsequently converted and expressed as ppm cyanidin-3-glucoside equivalents (ppm C3GE; mg kg^{-1} dry weight basis).

Total Protein Content

Total protein content was determined using the Kjeldahl method following Desta *et al*. (2022). Harvested seeds were first oven-dried to a constant weight, ground into a fine flour, and homogenized prior to analysis. Approximately 0.5 g of the seed flour sample was digested with 12 mL of concentrated H_2SO_4 and two selenium catalyst pellets using a Kjeltec auto-digester (FOSS, Tecator, Hoganas, Sweden) for 1 h. After digestion, the mixture was cooled and subjected to distillation and titration. Total protein content was calculated from the total nitrogen concentration using a conversion factor of 6.25 (N × 6.25). Protein content was expressed as a percentage (%) on a dry-weight basis. All samples were analyzed in triplicate, and the mean values were used for statistical analysis.

RESULTS AND DISCUSSION

Analysis of variance (ANOVA) revealed that the combination between boron application and liquid biofertilizer (LBF) significantly affected flavonoid content in black soybean seeds ($p < 0.05$). As shown in Figure 1, the highest flavonoid content was recorded under the application of 7.5 kg ha^{-1} boron combined with 10 mL L^{-1} LBF (P5), reaching 59.63 mg QE 100 g^{-1} DW, which differed significantly from all other treatment combinations according to Tukey's Honest Significant Difference (HSD) test. The lowest flavonoid content was observed in P4 (40.47 ppm mg QE 100 g^{-1} DW). Increasing boron application from 2.5 to 7.5 kg ha^{-1} at a constant LBF concentration of 10 mL L^{-1} resulted in a progressive increase in flavonoid accumulation. However, increasing the LBF concentration from 10 to 15 mL L^{-1} at the same boron level generally reduced flavonoid content.

Tukey's HSD test further indicated that P1 (48.93 mg QE 100 g^{-1} DW) and P2 (49.30 mg QE 100 g^{-1} DW) were not significantly different from each other, whereas all remaining treatment combinations differed significantly. These findings suggest that boron supplementation exerted a stronger influence on flavonoid biosynthesis when applied together with the lower LBF concentration (10 mL L^{-1}), while excessive LBF application may have reduced the stimulatory effect of boron on phenolic metabolism.

A similar trend was observed for anthocyanin content (Figure 2). Analysis of variance revealed a significant combination between boron application and liquid biofertilizer (LBF) on anthocyanin accumulation in black soybean seeds ($p < 0.05$). The highest anthocyanin content was obtained under the combination of 7.5 kg ha^{-1} boron and 10 mL L^{-1} LBF (P5), reaching 555 ppm, whereas the lowest value was recorded in 2.5 kg ha^{-1} B + 10 mL L^{-1} LBF (P1), with 270 ppm. According to Tukey's Honest Significant Difference (HSD) test at the 5% significance level, all treatment combinations differed significantly from one another. Increasing boron application from 2.5 to 7.5 kg ha^{-1} under 10 mL L^{-1} LBF consistently enhanced anthocyanin accumulation, whereas increasing the LBF concentration from 10 to 15 mL L^{-1} at the same boron level generally reduced anthocyanin content. These findings indicate that anthocyanin biosynthesis in black soybean seeds was strongly regulated by the interaction between micronutrient availability and rhizosphere microbial activity.

Physiologically, boron plays important structural and biochemical roles in plant metabolism. Boron forms borate diester cross-links with rhamnogalacturonan II in cell wall pectins, contributing to cell wall integrity and membrane stability (Mehboob *et al*., 2022). Boron has also been associated with carbohydrate transport and assimilate distribution within plants, which may indirectly influence seed metabolic processes (Abati *et al*., 2022). In the present study, the higher flavonoid and anthocyanin contents observed under increased boron application may indicate that adequate boron availability favored metabolic conditions associated with secondary metabolite accumulation. Boron is an essential micronutrient involved in cell wall structure, membrane stability, assimilate transport, and several metabolic processes that influence plant growth and development (Pereira *et al*., 2021; Reguera and Camacho-Cristóbal, 2023). Previous studies have also highlighted the close relationship between plant nutritional status and the accumulation of phenolic compounds, including flavonoids and anthocyanins, which are regulated by environmental and physiological factors (Shi *et al*., 2023).

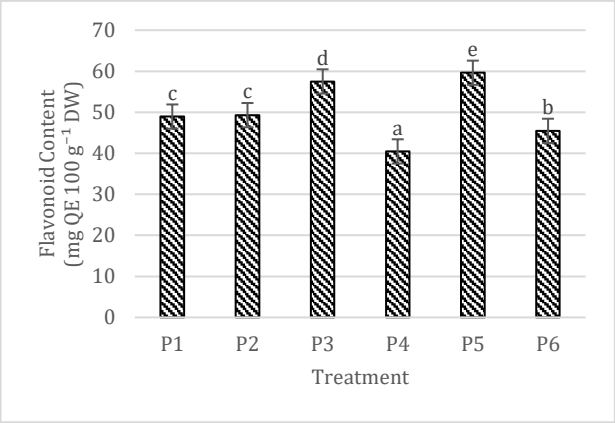


Figure 1. Figure 1. Total flavonoid content of black soybean seeds as affected by boron and liquid biofertilizer (LBF) application. Values represent mean ± SE (n = 3). Different letters above the bars indicate significant differences according to Tukey's Honest Significant Difference (HSD) test at $p < 0.05$.

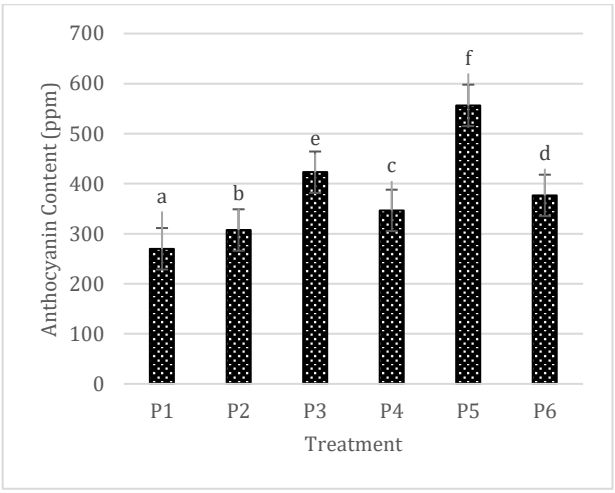


Figure 2. Total anthocyanin content of black soybean seeds as affected by boron and liquid biofertilizer (LBF) application. Values are presented as mean ± SE (n = 3). Different letters above the bars indicate significant differences among treatments according to Tukey's Honest Significant Difference (HSD) test at $p < 0.05$.

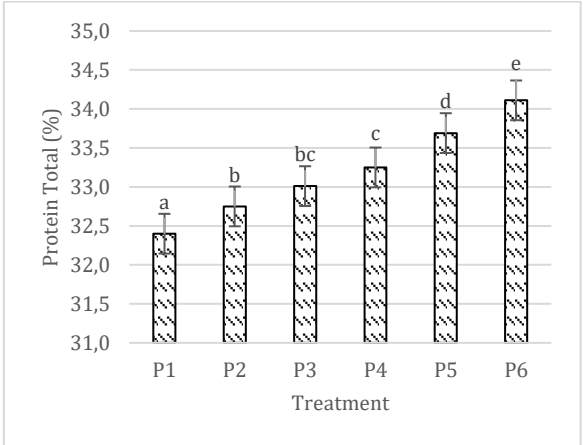


Figure 3. Total protein content (%) of black soybean seeds as affected by boron and liquid biofertilizer (LBF) application. Values are presented as mean ± SE (n = 3). Different letters above the bars indicate significant differences among treatments according to Tukey's Honest Significant Difference (HSD) test at $p < 0.05$.

Since anthocyanins are predominantly localized in the seed coat of black soybean, the enhanced anthocyanin content observed in this study may be associated with improved physiological conditions during seed development under adequate boron supply. However, the specific mechanisms underlying these responses were not directly evaluated and therefore require further investigation.Flavonoids and anthocyanins are synthesized via the phenylpropanoid pathway originating from phenylalanine, with phenylalanine ammonia-lyase (PAL) acting as a key regulatory enzyme controlling carbon flux into secondary metabolism (Chatterjee and Bandyopadhyay, 2017). The enhanced accumulation observed under P5 suggests that sufficient boron supply, combined with moderate microbial stimulation, optimizes PAL activity and phenylpropanoid flux. Microorganisms present in LBF improve nutrient solubilization, stimulate phytohormone production, and enhance nitrogen availability through biological processes in the rhizosphere (Allouzi *et al*., 2022). Increased nitrogen availability supports amino acid biosynthesis, including phenylalanine, thereby strengthening the biochemical foundation for flavonoid and anthocyanin synthesis (Oral, 2024).

The reduction in flavonoid and anthocyanin content observed at the higher LBF concentration (15 mL L^{-1}) suggests that increasing LBF application did not further enhance phenolic accumulation in black soybean seeds. In the present study, the highest flavonoid and anthocyanin contents were obtained under the combination of 7.5 kg ha^{-1} boron and 10 mL L^{-1} LBF, whereas increasing the LBF concentration to 15 mL L^{-1} resulted in lower values. This response may indicate that the stimulatory effect of LBF on secondary metabolite accumulation is concentration-dependent. Similar observations have been reported in previous studies, where moderate biofertilizer application promoted the synthesis of phenolic compounds, while higher application rates did not necessarily result in further increases (Chen *et al*., 2024; Tanveer *et al*., 2025).

Importantly, the elevated anthocyanin accumulation observed under the optimal treatment (P5) indicates that the combination of boron and liquid biofertilizer effectively promoted the synthesis and accumulation of phenolic compounds in black soybean seeds. Anthocyanins represent one of the major flavonoid groups responsible for the characteristic dark pigmentation of black soybean seed coats and are widely recognized as bioactive compounds with important nutritional value (Desta et al., 2022). The higher anthocyanin content obtained under P5 suggests that appropriate nutrient management can influence seed biochemical composition. These findings are consistent with the observed increase in total flavonoid content, indicating that boron and liquid biofertilizer may act synergistically in enhancing the accumulation of phenylpropanoid-derived metabolites in black soybean seeds. In this context, the liquid biofertilizer (LBF), which contains beneficial microorganisms including *Pseudomonas* sp. (1×10^8 CFU mL^{-1}), *Azotobacter* sp. (9.4×10^8 CFU mL^{-1}), *Lactobacillus* sp. (7.9×10^8 CFU mL^{-1}), *Azospirillum* sp. (5.5×10^8 CFU mL^{-1}), *Rhizobium* sp. (1.3×10^8 CFU mL^{-1}), *Nitrobacter* sp. (3.1×10^8 CFU mL^{-1}), and *Trichoderma* sp. (2.9×10^8 CFU mL^{-1}), contributes through multiple mechanisms such as biological nitrogen fixation, nutrient solubilization, phytohormone production, and improved nutrient uptake efficiency. These microbial activities enhance nutrient availability and metabolic activity in the rhizosphere, thereby supporting the biosynthesis of phenylpropanoid-derived compounds, including anthocyanins and other flavonoids.

In contrast, total protein content was significantly affected by the combination between boron and liquid biofertilizer (LBF) application (Figure 3). The highest protein content was observed under 7.5 kg ha^{-1} B + 15 mL L^{-1} LBF (P6), reaching 34.10%, whereas the lowest value was recorded under 2.5 kg ha^{-1} B + 10 mL L^{-1} LBF (P1), with 32.40%. According to Tukey's Honest Significant Difference (HSD) test at the 5% significance level, P6 produced significantly higher protein content than all other treatments. However, no significant differences were observed between P2 and P3, as well as between P3 and P4. Overall, increasing boron and LBF application tended to enhance protein accumulation in black soybean seeds. These results suggest that primary metabolism, particularly nitrogen assimilation and storage protein synthesis, responded positively to increased nutrient availability. Liquid biofertilizer enhances biological nitrogen fixation and nutrient mineralization through beneficial microorganisms such as *Azotobacter* sp., *Azospirillum* sp., *Rhizobium* sp., and *Nitrobacter* sp., thereby increasing nitrogen availability in the rhizosphere (Allouzi *et al*., 2022). Since nitrogen is a fundamental component of amino acids and proteins, improved nitrogen supply directly promotes seed protein accumulation

(Barunawati *et al*., 2013). In addition, *Pseudomonas* sp. and *Trichoderma* sp. improve root development and nutrient uptake efficiency, while *Lactobacillus* sp. contributes to nutrient cycling and rhizosphere conditioning, further supporting plant nutrient acquisition. Furthermore, boron contributes to membrane stability and nutrient translocation, supporting efficient nitrogen uptake and assimilation during seed development.

The contrasting response patterns between secondary metabolites and protein content reflect a metabolic trade-off between primary and secondary pathways. Secondary metabolite biosynthesis requires substantial carbon skeletons and reducing power derived from photosynthesis (Oral, 2024), whereas enhanced nitrogen availability favors protein synthesis and biomass formation. Consequently, the interaction between boron and the diverse microbial consortium in LBF modulates the allocation of metabolic resources, influencing whether carbon and nitrogen are directed toward protein accumulation or phenolic compound biosynthesis depending on nutrient balance.

These findings demonstrate that boron plays a multifaceted physiological role in black soybean, contributing not only to structural and reproductive processes (Aasim *et al*., 2022) but also to phenylpropanoid regulation and stabilization of anthocyanins in the seed coat. The combination between boron and liquid biofertilizer modulates key metabolic pathways by influencing the balance between primary metabolism (such as protein synthesis) and secondary metabolism (including phenolic compound accumulation). Through this metabolic regulation, the treatment enhances the nutritional quality of black soybean seeds by improving protein content while simultaneously increasing bioactive phenolic and anthocyanin compounds. As a result, the overall functional quality of the seeds is improved, particularly in terms of antioxidant capacity and health-promoting properties.

CONCLUSION

The combination of boron and liquid biofertilizer significantly influenced the biochemical composition of black soybean seeds. Treatment 7.5 kg ha^{-1} boron + 10 mL L^{-1} LBF (P5) resulted in the highest flavonoid and anthocyanin contents, while 7.5 kg ha^{-1} boron + 15 mL L^{-1} LBF (P6) produced the highest protein content. These results highlight the importance of optimizing nutrient and biofertilizer management to improve seed quality attributes in black soybean.

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AUTHORS CONTRIBUTIONS

NBW: Conceptualization, methodology, supervision, data interpretation, manuscript writing, review and editing, and project administration. NBW also served as the corresponding author and managed manuscript submission, revision, and communication with the journal. MRQ: Methodology development, statistical analysis, data interpretation, scientific validation, and manuscript review and editing. SLV: Investigation, field experiment implementation, sample preparation, laboratory analyses, data collection, data curation, preliminary statistical analysis, preparation of figures and tables, and manuscript drafting. AKN: Data interpretation, literature review, manuscript review and editing, and validation of scientific content and discussion.

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